DYNAMICS OF WAITING IN PIGEONS

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Two experiments used response-initiated delay schedules to test the idea that when food reinforcement is available at regular intervals, the time an animal waits before its first operant response (waiting time) is proportional to the immediately preceding interfood interval (linear waiting; Wynne & Staddon, 1988). In Experiment 1 the interfood intervals varied from cycle to cycle according to one of four sinusoidal sequences with different amounts of added noise. Waiting times tracked the input cycle in a way which showed that they were affected by interfood intervals earlier than the immediately preceding one. In Experiment 2 different patterns of long and short interfood intervals were presented, and the results implied that waiting times are disproportionately influenced by the shortest of recent interfood intervals. A model based on this idea is shown to account for a wide range of results on the dynamics of timing behavior.

Key words: linear waiting, temporal discrimination, sequential analysis, cyclic-interval schedules, response-initiated delay schedules, key peck, pigeons

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When an hedonic event such as a food delivery to a hungry subject occurs at regular intervals, behavior often reflects this periodicity. This was demonstrated in Pavlov's laboratory at the turn of the century (Feokritova, 1912, cited in Pavlov, 1928), and it has been much studied since, in both operant and Pavlovian settings (see Richelle & Lejeune, 1980, for a review). Recently, Staddon, Wynne, and Higa (1991), expanding on a suggestion of Ferster and Skinner (1957), argued that adaptation to temporal constraints may be responsible for the typical patterns of responding observed on many different schedules of reinforcement, not just those in which time is explicitly programmed (e.g., interval schedules).

After sufficient experience on periodic food schedules (such as fixed interval or fixed time), subjects usually develop a pattern of responding that takes the form of a post-

reinforcement pause or *waiting time* in each interfood interval (IFI) before operant responding begins. This waiting time is typically proportional to the IFI (Schneider, 1969). Skinner (1938) observed that "With a relatively short period of [temporal conditioning] depressions [i.e., postreinforcement pauses] begin to appear within a few days" (p. 125). He also noted that when the IFI was long, the development of pausing was "substantially retarded." Because of this lag in adaptation, most research on temporal schedules has centered on the steady-state properties of the behavior. In contrast, the present study tests an hypothesis about the dynamics of the process of initial adaptation to temporal schedules.

Several recent studies (Higa, Thaw, & Staddon, 1993; Higa, Wynne, & Staddon, 1991; Innis, Mitchell, & Staddon, 1993; Wynne & Staddon, 1988, 1992) have looked at the dynamics of the pausing process in pigeons using response-initiated delay (RID) schedules (technically, signaled chain or conjunctive fixed-ratio [FR] 1 fixed-time [FT] schedules). As shown in Figure 1, each IFI starts with the single response key illuminated red. A response to this key causes it to turn green for a schedule-controlled time (the food delay, *T*) prior to the delivery of food. The next IFI follows directly.

Wynne and Staddon (1988, 1992) showed that on these RID schedules, pigeons pause an approximately fixed fraction of the interfood interval *I* (where *I* is just the sum of the
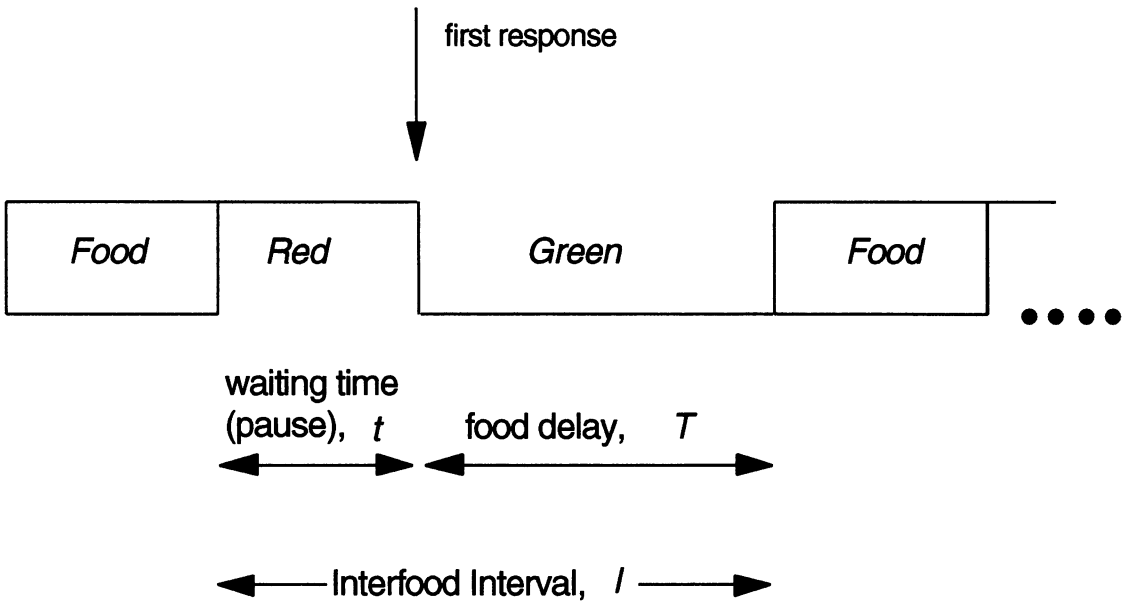
first response

Fig. 1.   One IFI of the response-initiated delay (RID) schedule.

waiting time, *t*, plus the subsequent programmed delay, *T*), irrespective of how the relationship between food delay and waiting time is programmed. Indeed, despite the color change on first response to a RID schedule, several studies have shown that waiting times so obtained are indistinguishable from those found on regular fixed-interval (FI) schedules in which the first response has no stimulus consequences (Shull, 1970; Wynne & Staddon, 1992). Innis et al. (1993) and Wynne and Staddon (1992) also demonstrated that waiting times on RID schedules are controlled by the IFI, and not the food delay, *T* (but see Capehart, Eckerman, Guilkey, & Shull, 1980). Moreover, the pigeons' waiting times tracked the IFIs even when these varied from trial to trial (Higa et al., 1991; Innis et al., 1993). Little sign was found of the gradual adjustment to each new IFI observed by Ferster and Skinner (1957). This suggested that at least some part of the dynamic process that allows adaptation to temporal schedules might be quite rapid. We termed this rapid adaptation of waiting times to IFIs obligatory *linear waiting* (Wynne & Staddon, 1988). The aim of the present experiments is to better understand this fast-acting process. We attempt to minimize the effects of slower processes by changing session parameters frequently.

The simplest theoretical possibility is that waiting is strictly a one-back process: Waiting time in IFI $N + 1$ is some function of the duration of the preceding IFI, N, that is, $t_{N+1} = f(I_N)$. The simplest form of dependence is linear, so the one-back linear-waiting hypothesis is just that:

$$t_{N+1} = AI_N + B, \qquad (1)$$

where A is the constant of proportionality ($0 < A < 1$) and B is a constant intercept of negligible magnitude (modal values from previous studies are $A = 0.2$, $B = 0$).

Wynne and Staddon (1988) tested a counterintuitive prediction of this hypothesis using an "autocatalytic" RID schedule in which the programmed delay, T was set proportional to the *preceding* IFI: $T_{N+1} = \omega I_N$. We argued that if waiting time, t_{N+1}, is proportional to the preceding IFI, only two outcomes are possible, depending on the value of the constant ω. If $\omega > 1/A$, waiting times in successive intervals should get longer and longer; if $\omega < 1/A$, waiting times should get shorter and shorter.

The results were in partial agreement with these predictions. At low values of ω, waiting times were very short; at high values of ω, waiting times were long and tended to increase in runs. But the fact that subjects rare-

ly stopped responding completely when exposed to large ω values implies that the preceding IFI is not the only determinant of waiting time. Our data are consistent with a dependence of waiting time on, for example, the weighted sum of the previous M IFIs (B is assumed to be negligible):

$$t_{N+1} = \sum_{k=0}^{M} A_k I_{N-k}, \qquad (2)$$

where A_k are weights for each IFI from 0 to M.

The aim of the present experiments was to explore the dependence of waiting time on preceding IFIs in the RID procedure. Our strategy was to present the pigeons with food delays that varied within a session, and to analyze the obtained waiting times to determine how they were influenced by IFIs further back in the past. In the first experiment we varied the duration of T from IFI to IFI in a more or less regular manner and then used simulations to see if waiting time, t_{N+1}, tracked IFI, I_N, in a manner consistent with one-back linear waiting, or whether the results implied effects of IFIs further back in the series. The second experiment allowed tests of specific hypotheses about how IFIs combine to influence waiting times.

EXPERIMENT 1: CYCLIC IFIS WITH ADDED NOISE

Several previous studies have shown that when IFIs vary regularly within a session, the pauses produced by pigeons track these changes (Higa et al., 1991; Innis, 1981; Innis et al., 1993; Innis & Staddon, 1970, 1971). Our aim here is to use this method to uncover the details of the dynamics of this process. Is waiting time controlled by IFIs in trials earlier than the immediately preceding one (is $M > 0$ in Equation 2)? We approach this question here by simulating the results to be expected on the basis of Equations 1 and 2 and comparing them with obtained waiting times from different input series.

Method

Subjects. Four experimentally experienced, locally acquired homing pigeons (*Columba livia*) of racing stock were used. They were held at 80% of their free-feeding weights by limiting access to food.

Apparatus. The experiment was run in a one-key cubic steel Skinner box with internal dimensions 33 cm on a side. A single response key (2.5 cm diameter), which could be transilluminated with red or green light, was mounted 21 cm above the floor in the center of the back panel. The food-hopper opening (2 cm diameter), set 7 cm above the floor in the center of the back wall, gave access to mixed food grains when the food hopper was raised. A houselight in the ceiling gave background illumination throughout the experiment. There was no need for a hopper light because the hopper opening projected 3 cm into the chamber. Food reward was 2-s access to mixed grains. A Commodore® VIC-20 microcomputer controlled experimental events and recorded the times of key pecks. Data were transferred to a larger computer for analysis.

Procedure. Each experimental session consisted of 100 IFIs of the RID procedure described above, one IFI of which is shown in Figure 1. In this experiment delay time, T, in the presence of the green stimulus varied from IFI to IFI according to the sinusoidal rule:

$$T_N = 10 + 5\sin(2N\pi/100) + \epsilon, \qquad (3)$$

where N is IFI number and ϵ is a noise term. Thus, when $\epsilon = 0$, successive values of T in a session followed a single cycle of a sine wave with a mean of 10 s and a range of 5 to 15 s. For the other three conditions, ϵ was derived by sampling from a rectangular random distribution ranging from 0 to 0.25, 0 to 0.5, or 0 to 2. In order to maintain a constant range of T values, each of the three T series obtained in this way was normalized to keep the overall range between 5 and 15 s. The four T series thus represent successively more degraded versions of the pure sine wave that comprised Condition 1. The four input series are the dashed lines in Figure 2. Each subject received one of these four T series each day so that each value was presented four times per subject. The order of the different series was quasi-randomized, as shown in Table 1.

Results

The key data here are the obtained series of waiting times (t values) for each T series. Figure 2 shows the four programmed T series, the mean series of waiting times, t, and the series of IFIs, I (the sum of the other two series) for Bird 15. The T and I series are
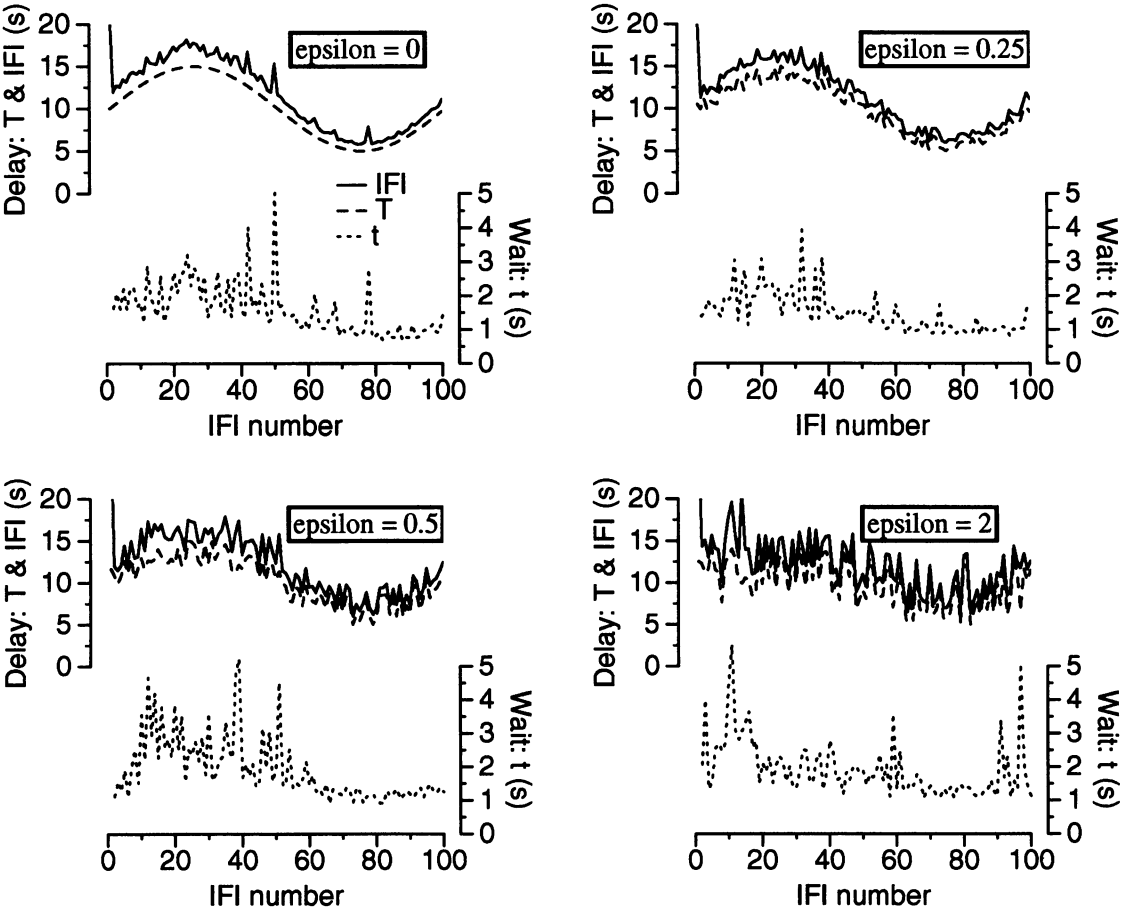
Fig. 2.   Each panel shows the input sequence of food delays (*T*, dashed lines), and interfood intervals (solid lines), plotted against the left *y* axis. The corresponding sequence of waiting times (*t*, dotted lines) is plotted against the right *y* axis. Values are averaged over the four sessions of each interfood interval series for Bird 15 in Experiment 1. The first waiting time and last interfood interval for each day are omitted.

plotted on a different ordinate scale than the *t* series. Visual inspection suggests that the waiting times track the IFIs, at least for the first three input series. As will be explained shortly, the data in Table 2 indicate that this subject tracked less effectively than Birds 195 and 280 and similarly to Bird 20.

The relationship of theoretical interest here is between the waiting times, *t*, and the IFIs, *I*. Figure 2 suggests a relationship between these variables. To quantify this impression we performed linear regressions of the series of *I* onto the series of *t*. Table 2 shows the best fits by the method of least squares to the equation

$$t_{N+1} = \alpha I_N + \beta \qquad (4)$$

for each of the four *T* series for each pigeon. This equation is identical to Equation 1 with the replacement of theoretical parameters *A* and *B* with empirical estimates α and β.

In performing the regression analysis from Equation 4 on these data, a possible confounding effect arises. Because $I_N = t_N + T_N$, a relationship between t_{N+1} and I_N could arise simply if *t* values tended to occur in runs of similar values. To control for this possibility, two further regression analyses were performed. The first was on the equation

$$t_{N+1} = \alpha T_N + \beta, \qquad (5)$$

which controls for the contribution of t_N to I_N. Finally a regression directly on the underlying sine wave was performed:

Table 1

Sequence of ϵ parameters for each pigeon in Experiment 1.

Condition (day)	Bird			
	15	20	195	280
1	0	2	0.5	0.25
2	0.25	0.5	2	0
3	0.5	0.25	0	2
4	2	0	0.25	0.5
5	0	2	0.5	0.25
6	0.25	0.5	2	0
7	0.5	0.25	0	2
8	2	0	0.25	0.25
9	0	2	0.5	0.5
10	0.25	0.5	2	0
11	0.5	0.25	0	2
12	2	0	0.25	0.5
13	0	2	0.5	0.25
14	0.25	0.5	2	0
15	0.5	0.25	0	2
16	2	0	0.25	0.5

$$t_{N+1} = \alpha\sin(2N\pi/100) + \beta. \qquad (6)$$

This tests whether the tracking by t values is really of the underlying sinusoid.

The results of these regression analyses for all subjects are shown in Table 2. Consider first the proportions of variance accounted for (r^2) by the three regression equations. Most of these values are similar for the three different regressions. It is not the case that the regressions of t onto I are inflated relative to the regressions of t onto T or the underlying sinusoid. Indeed, usually the regressions onto I produce lower r^2 values than do the other two regression equations, indicating that there can be no inflation of these values due to the relationship between t_N and I_N.

Table 2 shows three things about the relationship between t_{N+1} and I_N. First, β is never significantly different from zero (except for Bird 195 in Condition $\epsilon = 2$; see the 95% confidence intervals). Second, values of α are around 0.2 (a little lower for Bird 15), a value compatible with what has been found in previous studies (Higa et al., 1991; Wynne & Staddon, 1988, 1992). Third, the proportion of variance (r^2) accounted for by each regression equation decreases as the value of ϵ increases (i.e., the noisier series are less well fitted by this model). The relationship between r^2 and ϵ is included in the bottom panel of Figure 3.

The relationship between r^2 and ϵ for the regression onto I shown in Table 2 and Figure

3 does not appear to be consistent with a simple one-back process. Intuitively, a one-back process should be able to track a noisy IFI series just as well as a smooth one. Our data, on the contrary, show that the larger the value of the noise term, ϵ, the poorer the tracking. However, intuition is often a poor guide, especially because we must also take into account that, in addition to the noise in the IFI series, the linear waiting process will itself be noisy. We therefore performed a number of simulations of different types of noisy linear waiting, to see how the pattern of correlations for the simulated data compared with the correlations from the pigeon data at different values of the ϵ parameter. The pattern of results from all models assuming an influence of IFIs further than one back ($M > 0$ in Equation 2) converged on an analogous relationship between r^2 and ϵ, and therefore we present here the results from just two noisy models: a one-back process and a three-back process ($M = 2$ in Equation 2). Our method was to generate simulated data with these two processes and compare the pattern of correlations between simulated t_{N+1} and I_N with those obtained from the pigeon data.

In the first simulation, a t series was created from a noisy first order linear waiting process according to Equation 7:

$$t_{N+1} = (A + \tau)I_N. \qquad (7)$$

This is simply Equation 1 with $B = 0$ and the addition of a Gaussian noise term τ. A, the constant of proportionality, was set equal to 0.20 (the relations of interest do not depend on the value of A). Note that the noise here is added to A in Equation 1 (rather than to I) to ensure that the standard deviation of the distribution of the waiting times for constant I is proportional to their mean, as the Weber law property of temporal discrimination requires (cf. Gibbon, 1977; Staddon, 1965).

Our second simulation was based on Equation 2, with $M = 2$ and $A_0 = A_1 = A_2 = 0.2/3$, and Gaussian noise added as in Equation 7. Equation 8 is an example of a three-back linear waiting process:

$$t_{N+1} = [(A + \tau)/3](I_N + I_{N-1} + I_{N-2}). \qquad (8)$$

Figure 3 shows the r^2 values for the regressions of t_{N+1} onto I_N for each value of ϵ. For the one-back simulation (Equation 7), we see that, with no noise in the simulation, r^2 is 1.0 for all values of ϵ. This illustrates the fact that

Table 2

Linear regression of wait series, t_{N+1}, onto IFI series, I_N, delay series, T_N, and onto the underlying sinusoid, $\sin(2N\pi/100)$, for each bird in Experiment 1 (averaged over each ϵ value). Mean parameter values are shown with associated 95% confidence intervals in brackets. $df = 97$ in all cases.

Bird	ϵ	r^2	Model
15	0	.36	$t_{N+1} = 0.11[0.08 \to 0.14]I_N \quad + 0.32[-0.03 \to 0.68]$
	0.25	.47	$t_{N+1} = 0.11[0.09 \to 0.13]I_N \quad + 0.23[-0.05 \to 0.52]$
	0.5	.23	$t_{N+1} = 0.12[0.07 \to 0.16]I_N \quad + 0.48[-0.07 \to 1.04]$
	2	.10	$t_{N+1} = 0.11[0.05 \to 0.18]I_N \quad + 0.62[-0.24 \to 1.48]$
	0	.40	$t_{N+1} = 0.14[0.10 \to 0.17]T_N \quad + 0.24[-0.11 \to 0.59]$
	0.25	.53	$t_{N+1} = 0.14[0.11 \to 0.16]T_N \quad + 0.14[-0.13 \to 0.41]$
	0.5	.34	$t_{N+1} = 0.20[0.15 \to 0.26]T_N \quad - 0.17[-0.78 \to 0.43]$
	2	.08	$t_{N+1} = 0.14[0.05 \to 0.23]T_N \quad + 0.63[-0.32 \to 1.58]$
	0	.40	$t_{N+1} = 0.68[0.51 \to 0.84]\sin(2N\pi/100) + 1.60[1.49 \to 1.72]$
	0.25	.50	$t_{N+1} = 0.58[0.46 \to 0.70]\sin(2N\pi/100) + 1.50[1.41 \to 1.58]$
	0.5	.45	$t_{N+1} = 0.90[0.70 \to 1.10]\sin(2N\pi/100) + 1.92[1.78 \to 2.06]$
	2	.11	$t_{N+1} = 0.58[0.24 \to 0.92]\sin(2N\pi/100) + 2.02[1.78 \to 2.26]$
20	0	.39	$t_{N+1} = 0.20[0.15 \to 0.25]I_N \quad + 0.36[-0.37 \to 1.10]$
	0.25	.23	$t_{N+1} = 0.22[0.14 \to 0.30]I_N \quad + 0.19[-0.92 \to 1.30]$
	0.5	.26	$t_{N+1} = 0.20[0.13 \to 0.27]I_N \quad + 0.41[-0.55 \to 1.36]$
	2	.06	$t_{N+1} = 0.12[0.03 \to 0.21]I_N \quad + 1.21[-0.01 \to 2.44]$
	0	.61	$t_{N+1} = 0.43[0.36 \to 0.50]T_N \quad - 1.31[-0.58 \to -2.05]$
	0.25	.40	$t_{N+1} = 0.47[0.35 \to 0.58]T_N \quad - 1.57[-0.38 \to -2.75]$
	0.5	.37	$t_{N+1} = 0.37[0.28 \to 0.47]T_N \quad - 0.70[-1.73 \to 0.32]$
	2	.14	$t_{N+1} = 0.28[0.14 \to 0.41]T_N \quad - 0.02[-1.45 \to 1.41]$
	0	.61	$t_{N+1} = 2.16[1.82 \to 2.51]\sin(2N\pi/100) + 3.02[2.77 \to 3.26]$
	0.25	.39	$t_{N+1} = 2.01[1.51 \to 2.51]\sin(2N\pi/100) + 3.03[2.67 \to 3.38]$
	0.5	.45	$t_{N+1} = 1.58[1.23 \to 1.92]\sin(2N\pi/100) + 3.11[2.87 \to 3.36]$
	2	.12	$t_{N+1} = 0.97[0.46 \to 1.49]\sin(2N\pi/100) + 2.73[2.36 \to 3.09]$
195	0	.48	$t_{N+1} = 0.18[0.14 \to 0.22]I_N \quad + 0.01[-0.48 \to 0.51]$
	0.25	.43	$t_{N+1} = 0.21[0.16 \to 0.25]I_N \quad - 0.23[-0.83 \to 0.36]$
	0.5	.33	$t_{N+1} = 0.17[0.12 \to 0.22]I_N \quad + 0.00[-0.64 \to 0.65]$
	2	.14	$t_{N+1} = 0.09[0.05 \to 0.13]I_N \quad + 0.94[0.39 \to 1.50]$
	0	.57	$t_{N+1} = 0.26[0.21 \to 0.30]T_N \quad - 0.31[-0.79 \to 0.16]$
	0.25	.44	$t_{N+1} = 0.27[0.21 \to 0.33]T_N \quad - 0.43[-1.06 \to 0.21]$
	0.5	.43	$t_{N+1} = 0.27[0.21 \to 0.33]T_N \quad - 0.56[-1.20 \to 0.08]$
	2	.15	$t_{N+1} = 0.12[0.06 \to 0.17]T_N \quad + 0.87[0.30 \to 1.45]$
	0	.57	$t_{N+1} = 1.29[1.07 \to 1.51]\sin(2N\pi/100) + 2.27[2.11 \to 2.43]$
	0.25	.45	$t_{N+1} = 1.20[0.93 \to 1.46]\sin(2N\pi/100) + 2.25[2.07 \to 2.44]$
	0.5	.48	$t_{N+1} = 1.07[0.84 \to 1.29]\sin(2N\pi/100) + 2.17[2.01 \to 2.33]$
	2	.29	$t_{N+1} = 0.60[0.42 \to 0.79]\sin(2N\pi/100) + 2.03[1.89 \to 2.16]$
280	0	.56	$t_{N+1} = 0.23[0.19 \to 0.27]I_N \quad - 0.56[-1.10 \to -0.02]$
	0.25	.52	$t_{N+1} = 0.23[0.19 \to 0.27]I_N \quad - 0.55[-1.12 \to 0.01]$
	0.5	.49	$t_{N+1} = 0.21[0.17 \to 0.25]I_N \quad - 0.37[-0.93 \to 0.19]$
	2	.21	$t_{N+1} = 0.19[0.12 \to 0.26]I_N \quad + 0.27[-0.70 \to 1.23]$
	0	.54	$t_{N+1} = 0.30[0.25 \to 0.36]T_N \quad - 0.76[-1.35 \to -0.16]$
	0.25	.52	$t_{N+1} = 0.31[0.25 \to 0.37]T_N \quad - 0.87[-1.49 \to -0.24]$
	0.5	.45	$t_{N+1} = 0.26[0.20 \to 0.32]T_N \quad - 0.42[-1.03 \to 0.19]$
	2	.21	$t_{N+1} = 0.24[0.14 \to 0.33]T_N \quad + 0.29[-0.68 \to 1.27]$
	0	.54	$t_{N+1} = 1.51[1.23 \to 1.79]\sin(2N\pi/100) + 2.27[2.07 \to 2.47]$
	0.25	.57	$t_{N+1} = 1.43[1.18 \to 1.67]\sin(2N\pi/100) + 2.21[2.04 \to 2.39]$
	0.5	.48	$t_{N+1} = 1.03[0.81 \to 1.24]\sin(2N\pi/100) + 2.25[2.10 \to 2.41]$
	2	.24	$t_{N+1} = 0.96[0.62 \to 1.30]\sin(2N\pi/100) + 2.67[2.42 \to 2.91]$

a one-back process tracks all input series equally well. As we add more noise, the model's ability to track is degraded: The r^2s are lower and decrease with increasing ϵ, but only up to about $\epsilon = 0.5$; beyond this level there is little further decrease in the r^2. The fits of the model decrease with increases in ϵ up to a certain level because there are autocorre-
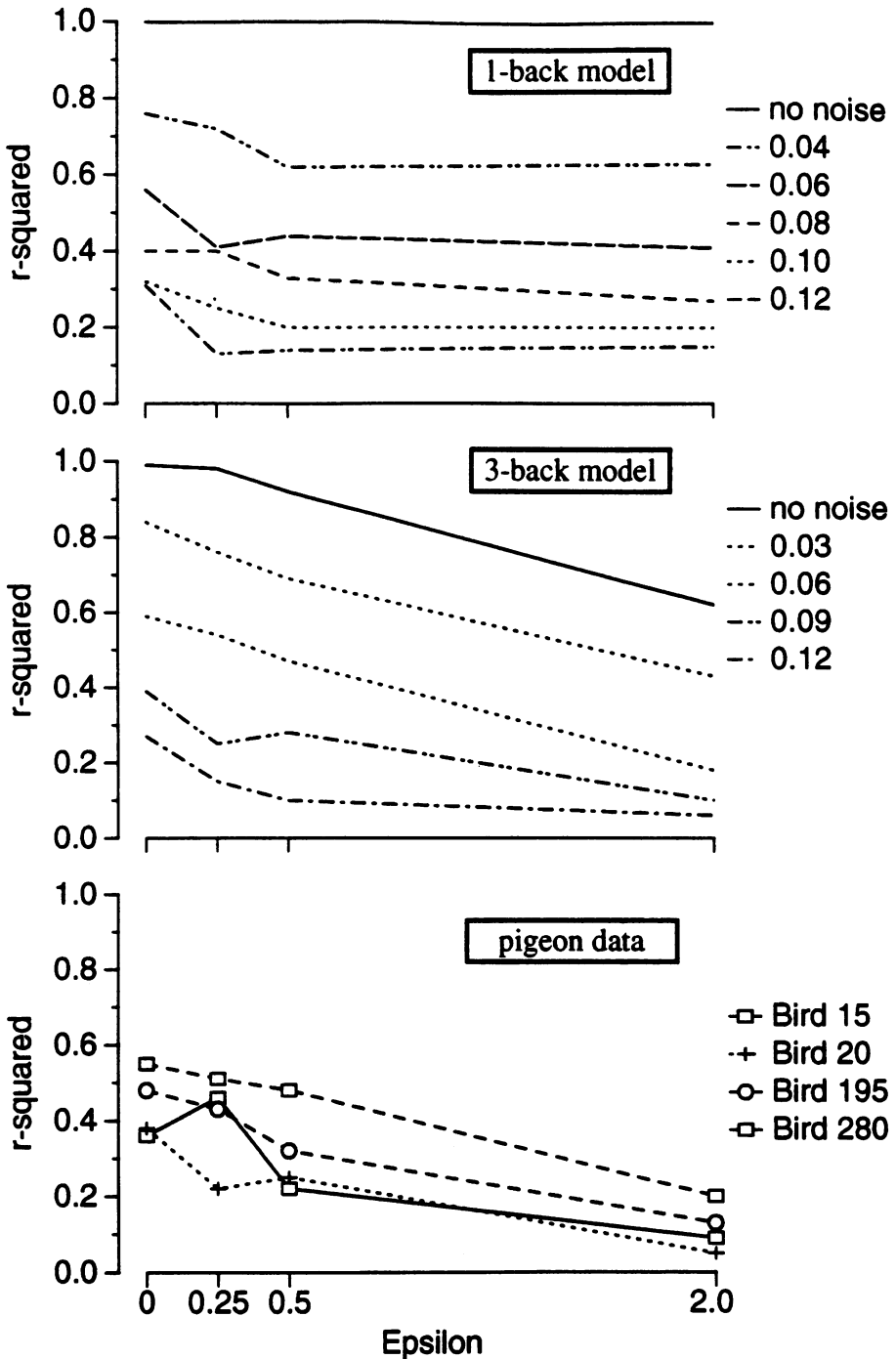
Fig. 3. Each panel shows the goodness of fit of the regression of waiting time in cycle $N + 1$ (t_{N+1}) onto IFI in cycle N (I_N). Top panel: results of a one-back linear waiting simulation (Equation 5); middle panel: results of a three-back simulation (Equation 6); bottom panel: results from subjects in Experiment 1. For both simulations the numbers in the legend are the standard deviations of the noise parameter τ. See text for further details.

lations in the sinusoid that underlies the T series. These autocorrelations in the input series values inflate the input–output correlations at the lowest ϵ values.

The results of the simulations of Equation 8 are plotted in the middle panel of Figure 3. Here, the ability of the simulated t series to track the I series is influenced by the amount of noise in the input series even when there is no noise in the simulation; the goodness of fit of the no-noise simulation declines as ϵ increases. With or without noise in the simulation, the r^2s decrease throughout the range of ϵ studied here. As expected, a more than one-back process is progressively impaired in its ability to track increasingly noisy input series.

The bottom panel of Figure 3 shows the comparable r^2 values for the data from the 4 subjects in this experiment (taken from Table 2). These r^2 values decline throughout the range of ϵ values tested, in a way that approximates simulations from the $M = 2$ model in the center panel.

Discussion

Experiment 1 shows that pigeons can track periodically varying series of food delays, even when the series are degraded by varying amounts of noise, but the greater the noise, the worse the tracking. This degradation of the effectiveness of tracking does not level off, as predicted by one-back linear waiting, but rather continues as more and more noise is added to the input series. This pattern is consistent with the hypothesis that current waiting time is influenced by IFIs further than one back.

These results cannot be taken as strong support for the particular more-than-one-back model simulated here (Equation 8). Many models with $M > 0$ in Equation 2 show some decrement in tracking with increasing input noise. In Experiment 2 we attempt to distinguish between different more-than-one-back linear waiting models.

EXPERIMENT 2: LONG AND SHORT DELAYS

Experiment 1 has shown that one-back linear waiting is inadequate as a model of how waiting times track IFIs. It is not possible, however, to use the results of that experiment

to distinguish between different ways in which earlier IFIs might influence waiting times. The purpose of Experiment 2 was to test four different models of how earlier IFIs could contribute to waiting time.

Model 1: Moving-Average Linear Waiting

A simple possibility is that waiting times are controlled by the average of the last few IFIs. Equation 8 is an instantiation of moving-average linear waiting, which, in general, states that A_ks in Equation 2 are equal for all k; that is,

$$t_{N+1} = [A/(M + 1)] \sum_{k=0}^{M} I_{n-k}, \qquad (9)$$

with parameters defined as before. Thus the wait on cycle N is defined as a proportion (A) of the average of the IFIs over the last M cycles.

Model 2: Moving-Minimum Linear Waiting

A related alternative is that waiting time is controlled by a moving minimum of the last few IFIs. There is much independent evidence from a variety of schedules that pigeons' waiting times are disproportionately influenced by the shortest of a group of IFIs. Higa et al. (1991), Staddon et al. (1991), and Wynne and Staddon (1992) have argued for an asymmetry in the influence of long and short IFIs on RID schedules. A moving-minimum version of linear waiting can be expressed as

$$t_{N+1} = A \min_{k=0}^{M} I_{N-k}. \qquad (10)$$

Thus the wait on cycle N is defined as a proportion (A) of the shortest IFI over the last M cycles.

Model 3: Exponentially Weighted Moving-Average Linear Waiting

Killeen (1994) has argued that simple moving-average models are implausible because they weight all events in memory up to the size of the memory window equally, but events prior to that point have zero weight. A moving average model "may serve as a rough approximation to short-term memory, but its calculation is computationally intensive and shows a biologically implausible discontinuity at some point in the past" (Killeen, 1994, p.

107). This criticism would also apply to simple moving-minimum models such as Equation 10. Instead, Killeen has proposed a model of memory in which event weights decay exponentially. That is,

$$A_k = \lambda e^{-\lambda k}, \qquad (11)$$

where λ is a rate parameter determining how quickly earlier events are forgotten. The update rule for a new estimate of waiting time . based on this exponentially weighted moving average (EWMA: Killeen, 1981, 1994), where weights decay as in Equation 11, is simply

$$t_{N+1} = \gamma A I_N + (1 - \gamma) t_N, \qquad (12)$$

where all parameters are as defined above and γ is a parameter derived from λ that controls how memory decays: $\gamma = -\ln(1 - \lambda)$.

Model 4: Exponentially Weighted Moving-Minimum Linear Waiting

It is also simple to modify this model to give greater weight to shorter IFIs. A simple inversion of the I parameter (and reinversion of the output) is sufficient to make an EWMA model that is disproportionately influenced by shorter IFIs (cf. Killeen, 1984):

$$1/t_{N+1} = \gamma A/I_N + (1 - \gamma) t_N. \qquad (13)$$

We term this model the exponentially weighted moving minimum (EWMM).

Experiment 2 tests these four forms of linear waiting against each other by presenting different series made up of IFIs that are either long or short. Each series consists of repeating groups of four IFIs each. Each group of four contains from zero to four short IFIs. The remaining IFIs in each group are long. Obtained waiting times can be compared to those predicted in two different ways: (a) as overall session averages (i.e., an average collapsed over all IFIs in the session) and (b) averaged separately for each position in the set of four IFIs.

We consider first the predicted overall session average waiting times. If all the IFIs in each set of four are long, then, according to all the models under consideration, the individual waiting times will all be long and therefore the session average waiting time must also be long. Similarly, if all the IFIs in a session are short, then the waiting times must also be short under any model.

Outcomes become more interesting as we mix together short and long IFIs. If most of the IFIs are long but we mix a few short ones into the series, a moving-average model predicts that the session average waiting time will decrease in proportion to the ratio of short to long IFIs. This result (for the average waiting time over a session) is independent of the size of the window over which IFIs are averaged, as long as the window is much shorter than a session. This prediction is shown in the top left panel of Figure 4. (In all these simulations, the relations of interest are not dependent on the value of A, which is therefore fixed at 0.2.)

The top right panel of Figure 4 shows how session average waiting times decrease for moving-minimum linear waiting models with increasing window sizes. The moving-minimum models produce average waiting times that drop off rapidly as the proportion of short IFIs increases. A moving-minimum model with a window of four cycles, for example, drops off to the shortest possible average waiting time as soon as every fourth IFI is short.

As shown in the bottom left panel of Figure 4, the predictions from the EWMA model (for session average waiting times) are very similar to those of the moving-average model. This model also shows a linear decline in waiting times as the proportion of short IFIs is increased. This prediction is little affected by the choice of parameter value (γ).

The predictions for session average waiting times from the EWMM model are shown in the bottom right panel of Figure 4. These predicted values are similar to those of the simple moving-minimum model, but they show a less sudden drop in waiting time as the proportion of short IFIs is increased.

Figure 5 shows predicted waiting times averaged separately for each position in the set of four IFIs. Only predictions from the moving-minimum and EWMM models are included—the other two models were found to be nonviable after an analysis of session average waiting times (Figure 6). Where space permits, a dashed line (not to scale) indicates the changing pattern of long and short IFIs.

The first column of Figure 5 shows the predictions from moving-minimum linear waiting. Here only three window sizes are considered ($M = 2$, 3, and 4). In the degenerate case of a window size of one, the waiting
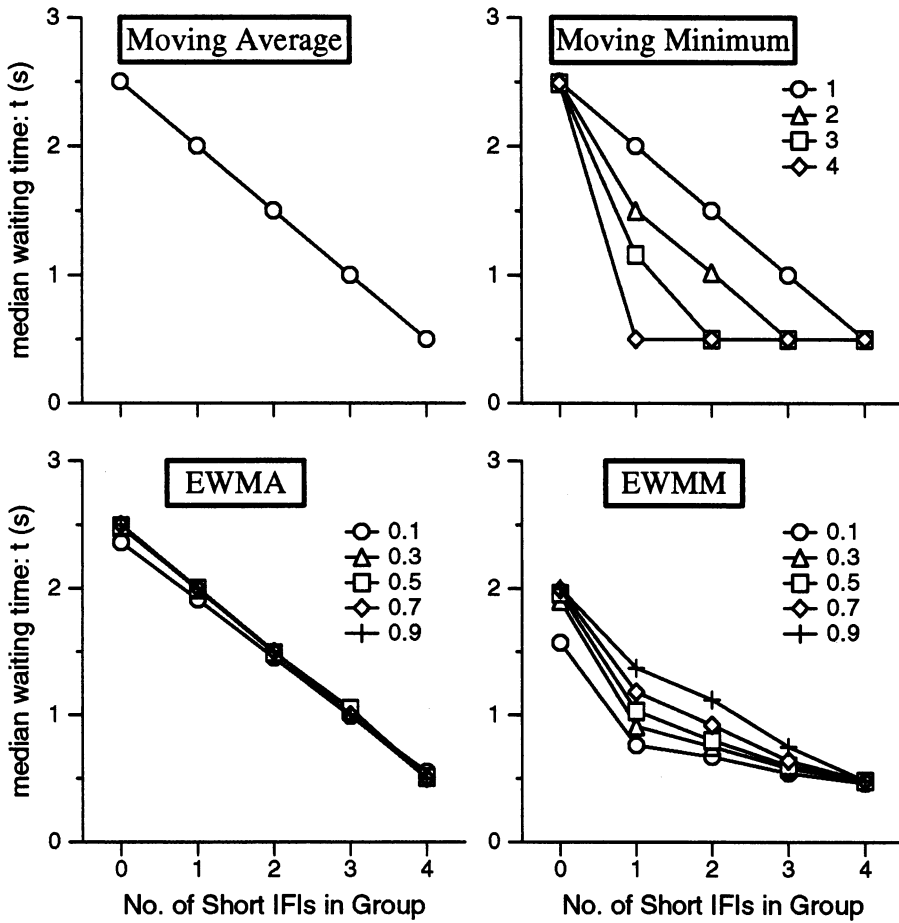
Fig. 4. Session average waiting times predicted by four models in Experiment 2. Top left panel: predictions from moving-average linear waiting. Top right panel: predictions from moving-minimum linear waiting. Parameter values shown are for M in Equation 10. Bottom left panel: predictions from the EWMA model. Parameter values are for γ in Equation 12. Bottom right panel: predictions from the EWMM model. Parameter values are for γ in Equation 13. See text for further details of models.

times would track IFIs perfectly. Window sizes greater than four behave the same as for a window size of four (squares in Figure 5)— no change in waiting time through the groups of four IFIs.

For moving-minimum linear waiting, waiting times track the series of IFIs; but rather than tracking smoothly, the model is more influenced by short IFIs than by long ones, and therefore drops off rapidly to shorter waiting times. Consider for example the condition in which $M = 3$. If any of the last three IFIs is short, then a short waiting time is emitted. Only if all three of the last IFIs are long is a long waiting time predicted. Thus only in the

one-short condition is any tracking observed at this parameter value.

For the EWMM model, values of γ determine the responsiveness of the model, but in general there is a progressive increase in waiting times for each successive long IFI and a progressive decrease for each short IFI. Similarly to the moving-minimum model, the behavior of this model is asymmetrical; each successive long IFI causes a gradual increase in waiting time, whereas a single short IFI causes a precipitous drop in waiting time.

Experiment 2 exposed pigeons to series of IFIs containing from zero to four short IFIs in every group of four IFIs, in order to test

Fig. 6. Session average waiting times obtained from 4 subjects in Experiment 2.

which of the four forms of linear waiting outlined above is most appropriate.

Method

Subjects and apparatus. Four homing pigeons (*Columba livia*) at 80% of their free-feeding weights, with experience on nontemporal studies, served as subjects. The same apparatus was used as in Experiment 1.

Procedure. Each IFI of this experiment was programmed as for Experiment 1 (see Figure 1). The first response on the red pecking key caused it to turn green for a time determined by the experimental program, before food reward was presented without the need for additional responding. The times in the presence of green were either long (L; 10 s) or short (S; 2 s). Each group of four consecutive IFIs consisted of a mixture of these two values. In each group of four, all the IFIs could be long; the first three could be long and the other short; the first two could be long and the last two short; the first one could be long and the other three short; or all the IFIs could be short. Thus the five cycle types were LLLL, LLLS, LLSS, LSSS, or SSSS. The number of short IFIs in each group of four IFIs was constant within a session and varied between daily sessions pseudorandomly for approximately seven sessions per condition, as shown in Table 3.

Results

Figure 6 includes the median wait times from each subject averaged over the last five
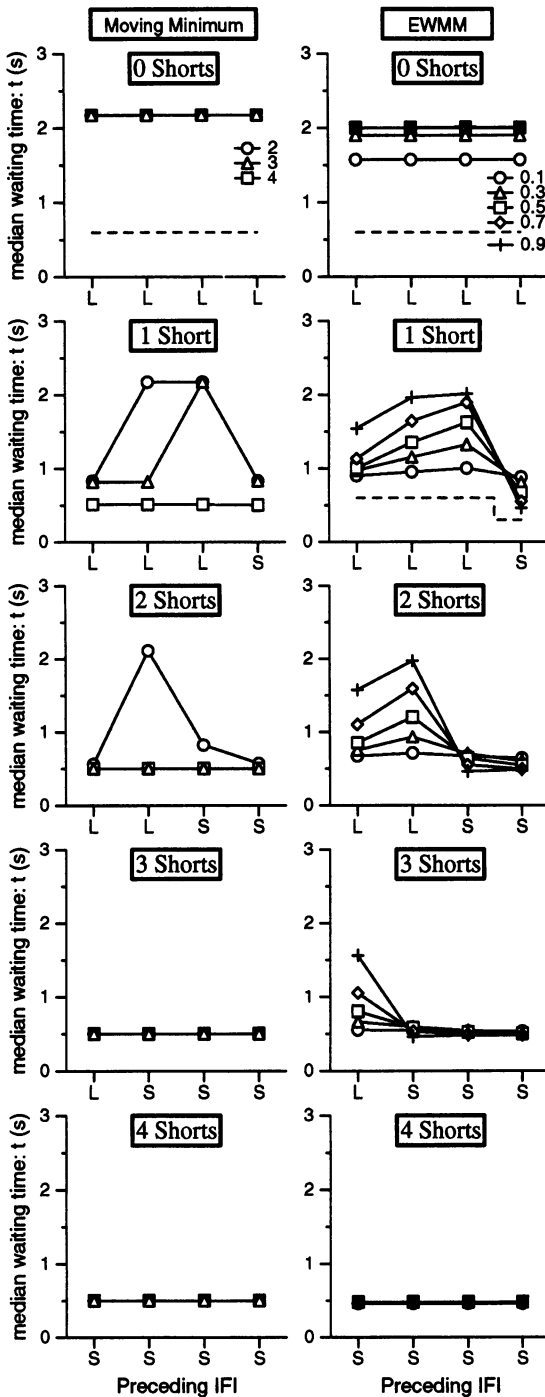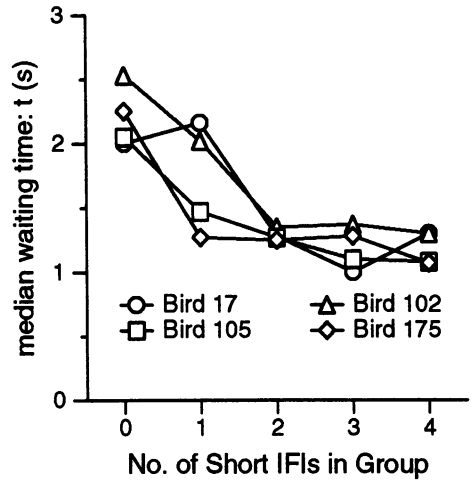

Fig. 5. Waiting times predicted for each point in the group of four IFIs for the moving-minimum and EWMM models in Experiment 2. For the moving-minimum model, the parameters shown are for M in Equation 10. For the EWMM model, the parameters shown are γ from Equation 13. Dashed lines indicate the magnitude of preceding IFIs (not to scale). See text for further details.

Table 3

Sequence of short food delays for each bird in Experiment 2.

Condition	Bird			
(day)	17	102	105	175
1	0	4	1	3
2	3	3	3	1
3	4	1	4	4
4	0	0	0	0
5	1	1	3	1
6	3	3	1	0
7	1	0	4	3
8	4	4	0	4
9	2	2	2	2
10	4	0	4	3
11	0	3	2	4
12	4	4	3	2
13	1	2	0	1
14	2	3	2	0
15	2	0	1	2
16	1	1	2	3
17	3	2	3	2
18	2	4	4	1
19	3	2	1	4
20	2	0	2	0
21	2	1	3	3
22	0	2	0	2
23	2	1	0	4
24	3	0	1	1
25	0	2	0	1
26	4	0	1	4
27	0	1	2	2
28	3	4	4	4
29	4	4	0	3
30	0	2	3	1
31	1	3	3	3
32	3		1	2
33	3		4	0
34	2		2	

sessions of each condition plotted analogously to the predicted values in Figure 4. By comparison with the other panels in Figure 4, it can be seen that neither the moving-average nor the EWMA models provide accurate accounts of the obtained results. However, the moving-minimum and EWMM models do capture features of the pigeon data.
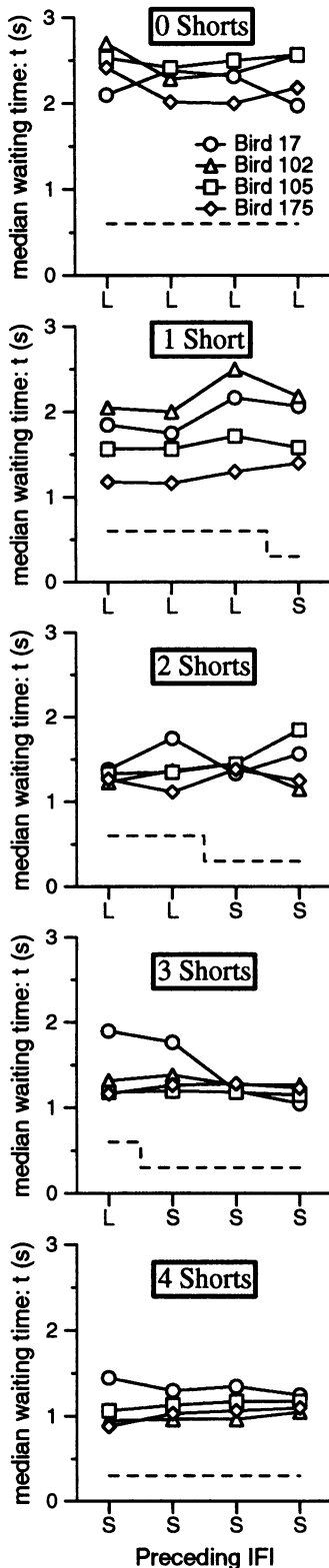
Pigeon waiting times were longest when there were zero short IFIs in each group of four IFIs. Once there were two or more short IFIs in each group, the obtained waiting times settled on a short value. Only when there was one short IFI in each group of four were there differences among the subjects. Bird 17 showed a waiting time similar to its waiting time with zero short IFIs (i.e., a long waiting time); this is consistent with moving-minimum linear waiting with a window of Size 3 or possibly the EWMM model with γ around 0.9. Bird 102 showed an intermediate waiting time in the one-short condition, which is also consistent with moving-minimum linear waiting with a window of Size 3 or the EWMM model with γ around 0.5. Birds 105 and 175 showed short waiting times in the one-short condition, implying a moving-minimum window of Size 4, or the EWMM model with $\gamma \le 0.3$. There are too few degrees of freedom for a statistical analysis of these patterns.

In Figure 7 median waiting times are averaged separately for each position in the group of four IFIs, analogous to Figure 5. For the zero-short and four-short conditions, all the IFIs in each group of four were long and short, respectively, and consequently the waiting times were all long or short. In the one-short condition, there was a gradual increase in waiting times through the three long IFIs, followed by a shorter waiting time after the short IFI. This pattern is consistent with both models shown in Figure 5, although the form is more like that of the EWMM model. As the number of short IFIs progressively increased, the subjects showed reduced responsiveness to conditions in the form of degraded tracking. In the two-short condition, the changes in waiting time were not very consistent. For three-short condition, the waiting times were mainly flat, except for Bird 17, whose waiting times were longer after the first two IFIs than after the subsequent ones. The changes in waiting time were not abrupt, as predicted by the moving-minimum model, but rather were smoother, more like the predictions from the EWMM model. The clearer tracking in conditions with few short IFIs than in conditions with more short IFIs (compare the one-short and three-short conditions) is also consistent with the EWMM model.

Discussion

The fact that the session average waiting times do not usually fall off gradually with an increasing proportion of short IFIs (Figure 6) is inconsistent with moving-average or EWMA linear waiting and supports the idea that shorter IFIs have a disproportionate influence on waiting time, either in the form of moving-minimum or EWMM linear waiting. The analysis of average waiting times at dif-

ferent positions in the four IFI groups (Figure 7) supported the EWMM but not the moving-minimum model. Both analyses suggest that for most subjects, values of γ less than 0.5 are most appropriate; this value indicates that the immediately preceding IFI contributes less than 50% to the next waiting time (the remaining control comes from earlier IFIs in an exponentially decaying series). The exception was Bird 17, which appears to have had a significantly larger value for γ, implying that the immediately preceding IFI was the main controlling factor for the present waiting time.

GENERAL DISCUSSION

These experiments show that pigeons are able to react rapidly to changes in temporal patterning of food delivery (at least at the short IFIs used here). It appears for our pigeons that waiting times were predominantly controlled not by the immediately preceding IFI, but by an average of the last few IFIs, where the calculation of that average is disproportionately influenced by shorter IFI values, and by more recent IFIs. A model implementing these features (the EWMM model, Equation 12) best accounted for the results of Experiment 2.

Experiment 1 demonstrated that pigeons can track different series of rapidly changing IFIs that vary randomly from day to day. However, their ability to track was degraded by noise added to the series of IFIs: The greater the noise, the poorer the tracking. This degradation implies that waiting time is affected by IFIs earlier than the immediately preceding one.

Experiment 2 tested four different forms of linear waiting that, in different ways, allowed IFIs earlier than one back to influence waiting time. The manner in which waiting times changed as different patterns of long and short IFIs were presented was inconsistent with models that assumed that an arithmetic mean moving average of the last few IFIs was

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Fig. 7. Obtained median waiting times for each bird in Experiment 2 averaged separately for each position in the group of four IFIs. Dashed lines indicate the magnitude of the preceding IFI (not to scale).

controlling waiting time. Models that give a disproportionate weight to shorter IFIs were, however, consistent with these results. The best descriptor of the obtained results was the EWMM model, which is based on an exponentially weighted moving average of the *inverted* IFI values. By inverting the IFI value (and then reinverting the output of the model), smaller IFI values come to have a disproportionate influence.

A version of linear waiting, such as EWMM, that gives a disproportionate weight to shorter IFIs can account for a wide range of apparently inconsistent phenomena in the literature on the dynamics of adaptation to time. In the introduction we described our autocatalytic schedule (Wynne & Staddon, 1988, Experiment 3). When the multiplier controlling the relationship between waiting time and IFI (ω) was small, the waiting times on this schedule reliably and rapidly became very short. When the ω values were large, the waiting times tended to increase, as expected from the one-back version of linear waiting, but in general the subjects' responding did not cease. The results from Experiment 2 clarified the reasons for this asymmetry. When the ω value was large, the EWMM process protected the subject against "inflationary" increases in waiting time, because any occasional short IFIs in the recent past put pressure on waiting times to remain short. Only when all recent IFIs were long was waiting time forced to increase. Thus, EWMM linear waiting permits rapid adaptation to temporal regularities in the environment but also protects subjects against the excessively long (in the sense that available reinforcers are missed) waiting times that would be produced under certain conditions by one-back or moving-average versions of linear waiting.

Staddon and associates (Innis & Staddon, 1970; Kello & Staddon, 1974; Staddon, 1967, 1969) tested pigeons on a variety of procedures in which fixed-interval (FI) schedules of two durations were programmed in repeating cycles. The general form of these schedules was 12 FI 1 min followed by *a* FI *x*-min schedules, where *ax* = 12. Thus each study consisted of cycles of 12 FI 1 min followed by a 12-min phase of a longer FI value. In one study the second half of each cycle consisted of six FI 2-min schedules (12 FI 1, 6 FI 2); in another the second half consisted

of four FI 3-min schedules (12 FI 1, 4 FI 3); and in a third the second half consisted of two FI 6-min schedules (12 FI 1, 2 FI 6). In all cases, waiting time during the long IFI part of the schedules differed little from waiting time during the short IFI part, even after extended training. Waiting times (postreinforcement pauses) throughout were close to 30 s, a value typical of the pauses on the FI 1-min schedules in the first half of each cycle. In the second half of each cycle, very slight increases in pause length were observed under the FI 2-min condition, and some pauses shorter than 30 s were observed in the FI 6-min intervals. Pausing on the FI 3-min schedules was identical to that found under the 12 FI 1-min schedules. Although we do not know whether the models developed here apply without modification to the substantially longer intervals used in these earlier studies, their results are nonetheless consistent with the present account. The counterintuitive result that pauses on the FI 2-min schedules were longer than those on FI 3-min and FI 6-min schedules is explained by the fact that, in these studies, the number of consecutive presentations of each FI value was inversely proportional to the length of the FI. If the subjects' pauses were determined by the shortest of recent IFIs, then control by the longer FIs can only be expected when enough of them occur consecutively that the EWMM process is no longer assessing any short FIs. When the FI value was 2 min, six presentations of this schedule were made, compared to only two presentations of the FI 6-min schedule. Thus the EWMM process assessed more long IFIs under the FI 2-min condition than under the FI 6-min condition, leading to longer pausing.

Innis (1981, Experiment 3, Condition 1) investigated schedules in which two FI values appeared in double alternation. The general form of these schedules was two FI 2Θ, two FI 6Θ, where Θ took on three values: 5, 15, and 30 s. In every case, waiting times failed to track changing FI values. Innis found a similar lack of temporal control in a condition in which long and short FI values were presented in strict alternation (Innis, 1981, Experiment 4). All of these results are consistent with EWMM linear waiting, because there were never sufficient consecutive long

IFI values to break the disproportionate influence of short IFIs.

Innis and Staddon (1971; see also Innis, 1981) compared cyclic-interval schedules with different forms of progressions. In three conditions, pigeons were exposed to a set of seven FIs increasing either from 20 to 80 s and back to 20 s in arithmetic steps; from 18 to 69 s and back in steps forming a logarithmic series; or in geometric steps from 3 to 176 s and back. Innis and Staddon concluded from visual inspection of the series of averaged postreinforcement pauses that the pigeons were tracking the FI values under all conditions at a lag of zero or one cycle. Tracking was clearer under the arithmetic and logarithmic cyclic schedules than under the geometric cyclic schedule. This would be expected from models that give a disproportionate weight to shorter IFIs, because the occasional long IFIs in a geometric series are ignored by models of this type.

Recently, Higa et al. (1993) trained pigeons on a sequence of IFIs of 15 s that, at an unpredictable point in the session, could change either to IFIs of 5 s (step down) or 45 s (step up). Higa et al. found that the subjects responded almost immediately to the step-down change in IFIs, but only gradually to a step-up change. Wynne and Staddon (1992, Experiment 5) found similar results in an analysis of adaptation to longer IFIs. Blocks of sessions in which the food delay on an RID schedule was 40 s alternated with blocks of sessions with food delays of 20 or 80 s. The development of waiting times appropriate to the 40-s food delay was much faster after previous experience with delays of 80 s than after delays of 20 s. These results are further evidence that short IFIs dominate over long ones in controlling waiting time.

There are some results that, at first glance, do not appear to be easily reconciled with the EWMM model. Higa et al. (1991, Experiment 3) simply presented pigeons with a series of 100 IFIs, 99 of which were of 15-s duration. Intercalated in this series was a single, randomly placed 5-s IFI "impulse." Three of 4 subjects showed a response to this impulse that consisted of a single shorter waiting time in the immediately following IFI and a return to waiting times consistent with the longer IFI value more or less immediately thereafter. One subject showed an only slightly shorter
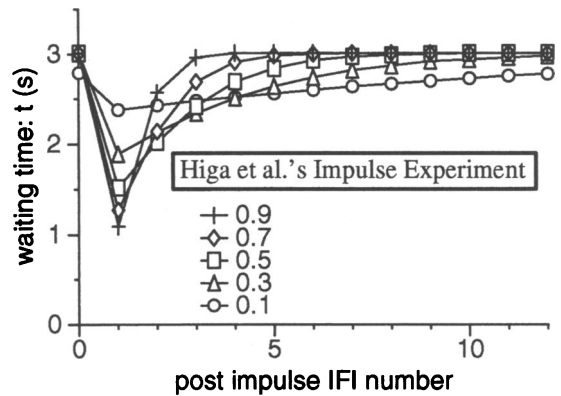

Fig. 8. Waiting times predicted from the EWMM model for Higa et al.'s (1991) impulse experiment. The impulse IFI is IFI 0. See text for further details.

waiting time in the postimpulse IFI, followed by a gradual return over three or four IFIs to the waiting time produced before the impulse. At first glance the evidence from the majority of these subjects appears to support one-back linear waiting and not the EWMM model.

However, the predictions of these models are often nonintuitive, so we performed a simulation of the behavior predicted by EWMM linear waiting. Figure 8 shows predicted waiting times from the EWMM model for a range of values of γ following a single short (5-s) IFI embedded in a series of longer (15-s) IFIs. Clearly, at higher values of γ (>0.7), the impact of the short IFI on waiting time was almost entirely confined to the first postimpulse IFI. Because in reality, the waiting times vary noisily from IFI to IFI, the apparent presence of an effect of the impulse on later IFIs for values of γ around 0.5 to 0.7 would probably not be detectable in empirical data. At values of γ less than 0.5, the impact of a short IFI lasts longer, but it is also much smaller in the first postimpulse IFI. This is precisely the pattern found for the one divergent subject in this experiment. Thus, on closer inspection, the EWMM model can account both for the short-lived but intense response to a single shorter IFI of the majority of subjects and also for the longer lasting, less intense response of the one remaining subject.

Is there a functional explanation for pigeons' special sensitivity to short IFIs? This sensitivity may be a conservative strategy that

reduces the possibility that a subject will miss an opportunity to get food. After all, there is an asymmetry in much operant behavior: The cost of making an operant response is usually very small, but the cost of missing an available food delivery is high. Hence, when in doubt, respond. There is also the logical fact that waiting time is defined by the *first* response in the IFI. As we have pointed out elsewhere (Higa et al., 1991; Wynne & Staddon, 1992), a small tendency to respond early in an IFI will dominate even a strong tendency to respond later, simply because an early response removes the possibility of producing a longer waiting time (this is the problem with relying exclusively on waiting time as a measure).

In conclusion, the studies reported here have shown that, although adaptation to changing IFIs can be rapid, nonetheless it is not typically one back, as we had originally proposed (Wynne & Staddon, 1988). Rather, a model proposing that the last few IFIs influence waiting time in such a way that short IFIs have a greater influence than longer ones can account for the data from these experiments and from a wide range of disparate results in the literature. Further research needs to analyze more closely the manner in which IFIs are combined and the factors that control the size of the window over which IFIs are measured.

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